SOCIAL LIFE AMONG THE INSECTS[1]

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LECTURE IV—ANTS, THEIR DEVELOPMENT, CASTES, NESTING AND FEEDING HABITS

II

There is throughout the animal kingdom, as I believe Espinas was the first to remark, a clear correlation on the one hand between a solitary life and carnivorous habits and on the other hand between social habits and a vegetable diet. The beasts and birds of prey, the serpents, sharks, spiders and the legions of predacious insects all lead solitary lives, whereas the herbivores, rodents, granivorous and frugivorous birds and plant-eating snails and insects are more or less gregarious. Man himself is quite unable to develop populous societies without becoming increasingly vegetarian. Compare, for example, the sparse communities of the carnivorous Esquimaux with the teeming populations of the purely vegetarian Hindoos. The reasons for these correlations are obvious, for plants furnish the only abundant and easily obtainable foods and, at least in the form of seeds and wood, the only foods that are sufficiently stable to permit of long storage. In the previous lectures I have shown that the social beetles and bees are strictly vegetarian and that the social wasps, though descended from highly predatory ancestors, are nevertheless becoming increasingly vegetarian like the bees. The ants exhibit in the most striking manner the struggle between a very conservative tendency to retain the precarious insectivorous habits of their vespine ancestors and a progressive tendency to resort more and more to a purely vegetable regimen as the only means of developing and maintaining populous and efficient colonies. Anthropologists have distinguished in the historical development of human societies six successive stages, designated as the hunting, pastoral, agricultural, commercial, industrial and intellectual. Evidently the first three, the hunting, pastoral and agricultural, are determined by the nature of the food and represent an advance from a primitive, mainly flesh-consuming to a largely vegetarian regimen. Lubbock showed that the same three stages occur in the same sequence in the phylogenetic history of the ants. At the present time we are able to give even greater precision to his outlines of this evolution.

[1] Lowell Lectures.

All the primitive ants are decidedly carnivorous, that is predatory hunters of other insects. That this must have been the character of the whole family during a very long period of its history is indicated by the retention of the insectivorous habit, in a more or less mitigated form, even in many of the higher ants. Always striving to rear as many young as possible, always hungry and exploring, the ants early adapted themselves to every part of their environment. They came, in fact, to acquire two environments, each peopled by a sufficient number of insects, arachnids, myriopods, etc., to furnish a precarious food-supply. Most of the ants learned to forage on the exposed surface of the soil and vegetation and became what we call epigæic, or surface forms, while a smaller number took to hunting their prey beneath the surface of the soil and thus became hypogæic, or subterranean. Many of the latter are very primitive but their number has been repeatedly recruited from higher genera, which by carrying on all their activities within the soil have found a refuge and surcease from a too strenuous competition with the epigæic species. We have here some very interesting cases of convergence, or parallel development, since the underground habit has caused the workers, which rarely or never leave their burrows, to lose their deep pigmentation and become yellow or light brown and to become nearly or quite blind. As will be evident in the course of my discussion, the tendency towards vegetarianism is apparent among both the epigæic and hypogæic forms.

The ants belonging to the oldest and most primitive subfamilies, the Ponerinæ, Dorylinæ and Cerepachyinæ and also to many of the lower genera of Myrmicinæ, feed exclusively on insects and therefore represent the hunting stage of human society. Owing to the difficulty of securing large quantities of the kind of food to which they are addicted, many of the species form small, depauperate colonies, consisting of a limited number of monomorphic workers. Many of these species lead a timid, subterranean life. In the size of their colonies, which may comprise hundreds of thousands of individuals, the Dorylinæ alone constitute a striking exception, but one which proves the rule. These insects, known as driver, army or legionary ants and very largely confined to Equatorial Africa and tropical America, are strictly carnivorous, but being nomadic and therefore foraging over an extensive territory, are able to obtain the amount of insect food necessary to the growth and maintenance of a huge and polymorphic population. They are the famous ants whose intrepid armies often overrun houses in the tropics, clear out all the vermine and compel the human inhabitants to leave the premises for a time. In Africa they have been known to kill even large domestic animals when they were tethered or penned up and thus prevented from escaping.

The pastoral stage is represented by a great number of Myrmicine and especially of Formicine and Dolichoderine ants which live very largely on "honey-dew." This sweet liquid, concerning the origin of which there was much speculation among the ancients, is now known to be the sap of plants and to become accessible to the ants in two ways. First, it may be excreted by the plants from small glands or nectaries ("extrafloral nectaries") situated on their leaves or stems, where it is eagerly sought and imbibed by the ants. Second, a much more abundant supply is made accessible by a great group of insects, the Phytophthora, comprising the plant-lice, scale-insects, mealy-bugs, leaf-hoppers, psyllids, etc., which live gregariously on the surfaces of plants. These Phytophthora pierce the integument of the plants with their slender, pointed mouth-parts and imbibe their juices which consist of water containing in solution cane sugar, invert sugar, dextrin and a small amount of albuminous substance. In the alimentary canal of the insects much of the cane sugar is split up to form invert sugar and a relatively small amount of all the substances is assimilated, so that the excrement is not only abundant but contains more invert and less cane sugar. This excrement or honey-dew either falls upon the leaves and is licked up by the ants or is imbibed by them directly while it is leaving the bodies of the Phytophthora. Many species of ants have learned how to induce the Phytophthora to void the honey-dew by stroking them with the antennæ, protect and care for them and even to keep them in specially constructed shelters or barns. Some ants have acquired such vested interests in certain plant-lice that they actually collect their eggs in the fall, keep them in the nests over winter and in the spring distribute the hatching young over the surface of the plants. Linnæus was therefore justified in calling the plant-lice the dairy-cattle of the ants ("*hæ formicarum vaccæ*"). This dairy business is, in fact, carried on in all parts of the world on such a scale and with so many species of Phytophthora that it constitutes one of the most harmful of the multifarious activities of ants. Their irrepressible habit of protecting and distributing plant-lice, scale-insects, etc., is a source of considerable damage to many of our cultivated plants and especially to our fruit-trees, field and garden crops. Ants mostly attend Phytophthora on the leaves and shoots of plants, but quite a number of species are hypogæic and devote themselves to pasturing their cattle on the roots. Thus our common garden ant (*Lasius americanus*) distributes plant-lice over the roots of Indian corn.

The habit of keeping Phytophthora was probably developed independently in many different genera, and it is easy to see how the habit of feeding by mutual regurgitation among the ants themselves might have led to the behavior I have been describing. Cer-

tainly the genera that have developed trophallaxis among the adult members of their colonies are the very ones which most assiduously attend the Phytophthora. And it is equally certain that the latter habit is very ancient, because it was already established among the ants of the Baltic Amber during Lower Oligocene times and that, as we have seen, was many million years ago.

The dairying habit has led to an interesting specialization in certain species known as "honey ants," which inhabit desert regions or those with long, dry summers. These ants have found it very advantageous to store the honey dew collected during periods of active plant growth, and as they are unable to make cells like those of wasps and bees, have hit upon the ingenious device of using the crops of certain workers or soldiers for the purpose. In all ants, as we have seen, the crop is a capacious sac, but in the typical honey ants it becomes capable of such extraordinary distention that the abdomen of the individuals that assume the rôle of animated demijohns or carboys, becomes enormously enlarged and perfectly spherical. Such "repletes" (Fig. 66) are quite unable to walk and therefore suspend themselves by their claws from the ceilings of the nest chambers. When hungry the ordinary workers stroke their heads and receive by regurgitation droplets of the honey dew with which they were filled during seasons of plenty. The condition here described, or one of less gastric distention, has been observed in desert or xerothermal ants in very widely separated regions and belonging to some nine different genera of Myrmicinæ, Formicinæ and Dolichoderinæ (Myrmecocystus and Prenolepis in the United States and Northern Mexico, Melophorus, Camponotus, Leptomyrmex and Oligomyrmex in Australia, Plagio-

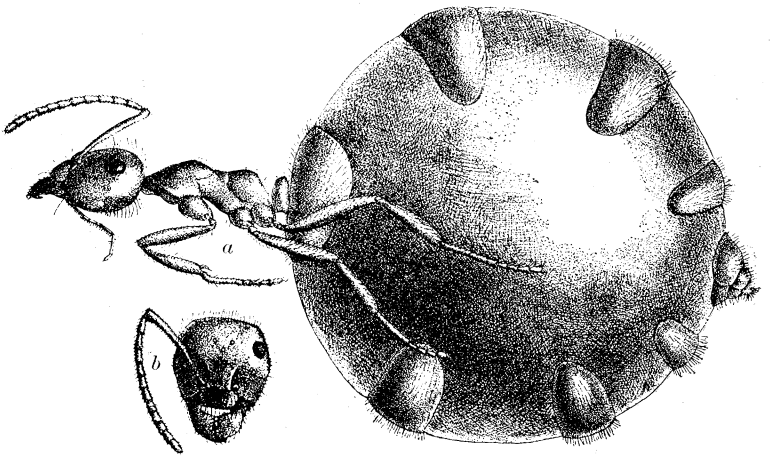

FIG. 66

Replete of honey ant (*Myrmecocystus melliger*) from Mexico. *a*, lateral aspect of insect; *b*, head from above.

lepis and Aëromyrma in Africa and Pheidole in Australia and the southwestern United States).

A more direct vegetarian adaptation is seen in many Formicidæ that inhabit the same desert or xerothermal regions as the honey ants. In such regions insect food is at no time abundant and is often so scarce that the ants are compelled to eat the seeds of the sparse herbaceous vegetation. At least a dozen genera, all Myrmicinæ, illustrate this adaptation: Pogonomyrmex, Veromessor, Novomessor and Solenopsis in America, Messor, Oxyopomyrmex, Goniomma, Tetramorium and Monomorium in the southern Palearctic region, Meranoplus in the Indoaustralian, Cratomyrmex and Ocymyrmex in the Ethiopian region and Pheidole (Fig. 57) in the warmer parts of both hemispheres. It was at one time believed that some of these ants actually sow around their nests the grasses and other herbaceous plants from which they gather the seeds, but this has been disproved. They are merely collected, husked and stored in special chambers or granaries in the more superficial and dryer parts of the formicary. Emery has shown that as food the proteids are preferred to the starchy portions of the seeds and are also fed to the larvæ. *Messor barbarus,* the ant to which Solomon refers, is one of these harvesters. Probably none of them disdains insect food when it can be had. Nevertheless the adaptation to crushing hard seeds is so pronounced in certain genera that the mandibles have become distinctly modified. Their blades have become broader and more convex and the head has been enlarged to accommodate the more powerful mandibular muscles. In certain forms (Pheidole, Messor, Novomessor, Holcomyrmex) the soldiers or major workers seem to function as the official seed-crushers of the colony.

The harvesting ants can hardly be regarded as true agriculturists because they neither sow nor cultivate the plants from which they obtain the seeds. Yet there is a group of ants which may properly be described as horticultural, namely the Attiini, a Myrmicine tribe comprising about 100 exclusively American species and ranging from Long Island, N. Y., to Argentina, though well represented by species only within the tropics. The tribe includes several genera (Cyphomyrmex, Apterostigma, Sericomyrmex, Myrmicocrypta, etc.) the species of which are small and timid and form small colonies with monomorphic workers, while others (Atta and Acromyrmex) are large and aggressive and form very populous colonies with extremely polymorphic workers. The Attas or parasol ants inhabit the savannas and forests of South and Central America, Mexico, Cuba and Texas. Their extensive excavations result in the formation of large mounds and often cover a considerable area (Fig. 67). According to Branner, a single mound of

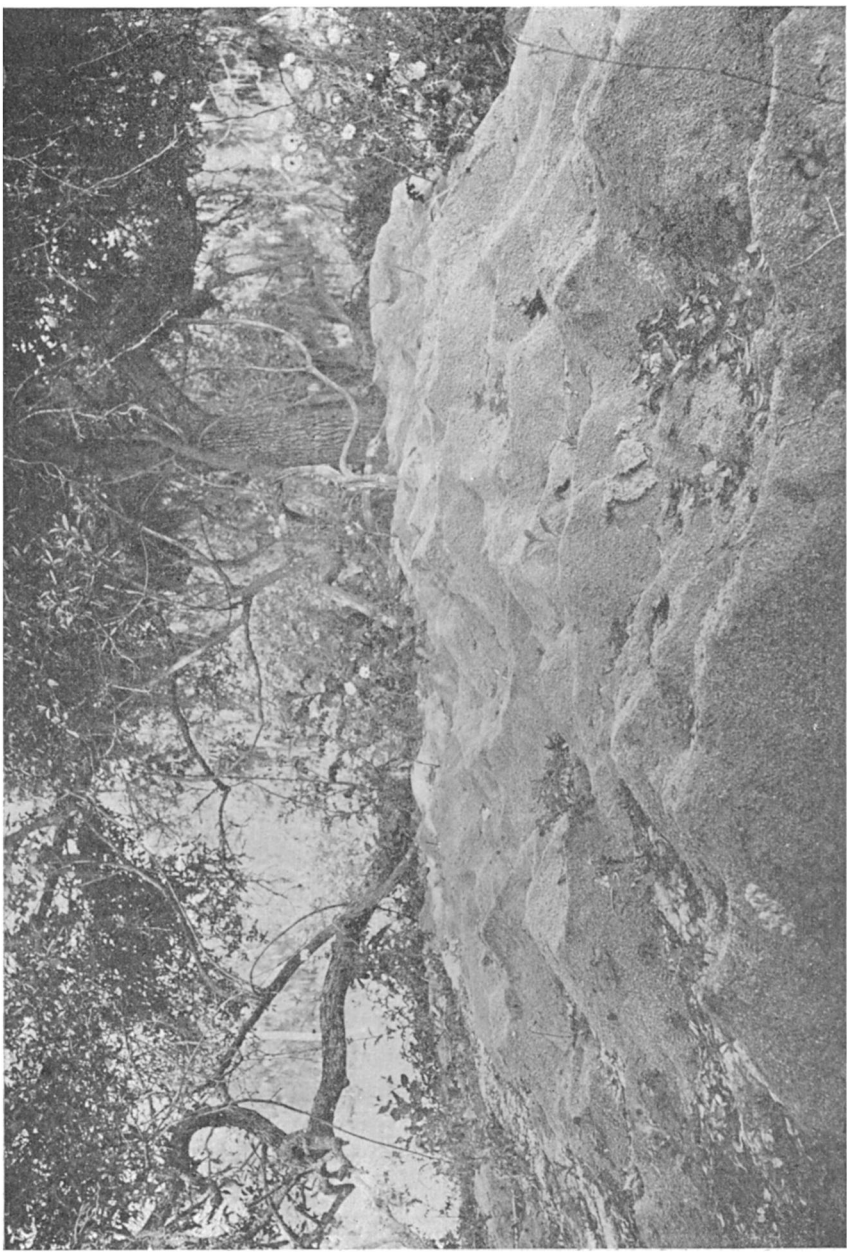

FIG. 67
Nest of the Texan leaf-cutting ant (*Atta texana*) at Victoria, Texas. (Photograph by S. J. Hunter.)

the common Brazilian *Atta sexdens* may contain as much as 265 cubic meters of earth, and the population of a colony of this species, according to Sampaio, may number from 175,000 to 600,000 individuals. Of course, the size of the mounds varies with the depth of the excavations, which are much shallower in the rain-forests than in the dry savannas. From their mounds the ants make well-worn paths through the surrounding vegetation and frequently defoliate bushes or trees, cutting large pieces out of their leaves and carrying them like banners to their nests. The pieces are then cut into smaller fragments and built up on the floors of the large nest chambers (Figs. 68 and 69) in the form of sponge-like

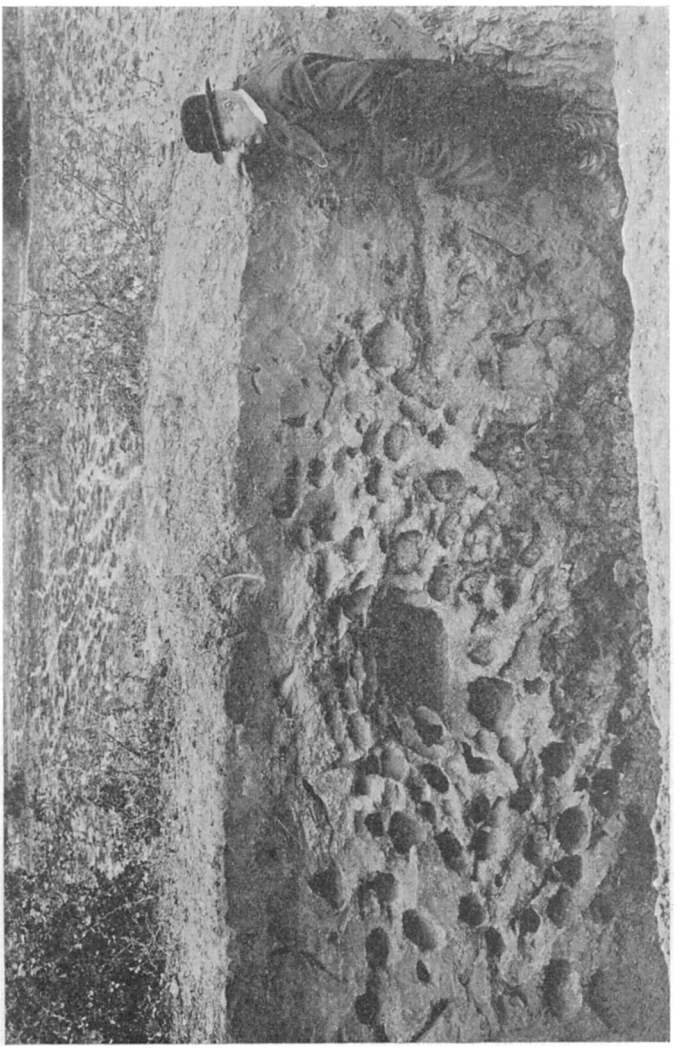

FIG. 68
Vertical section through the center of a nest of the Argentinian leaf cutter, *Atta vollenweideri*, showing the chambers containing the fungus gardens. (Photograph by Dr. Carlos Bruch).

masses, which become covered with a white, mould-like fungus mycelium (Figs. 70 and 71). The latter is treated in some unknown manner by the smallest, exclusively hypogæic caste of workers, so that the hyphæ produce abundant clusters of small, spherical dwellings, the bromatia (Fig. 72), which are eaten by the ants and fed to their larvæ. Each species of Attiine ant cultivates its own particular fungus and no other is permitted to grow in the nest. That the bromatia are really anomalous growths induced

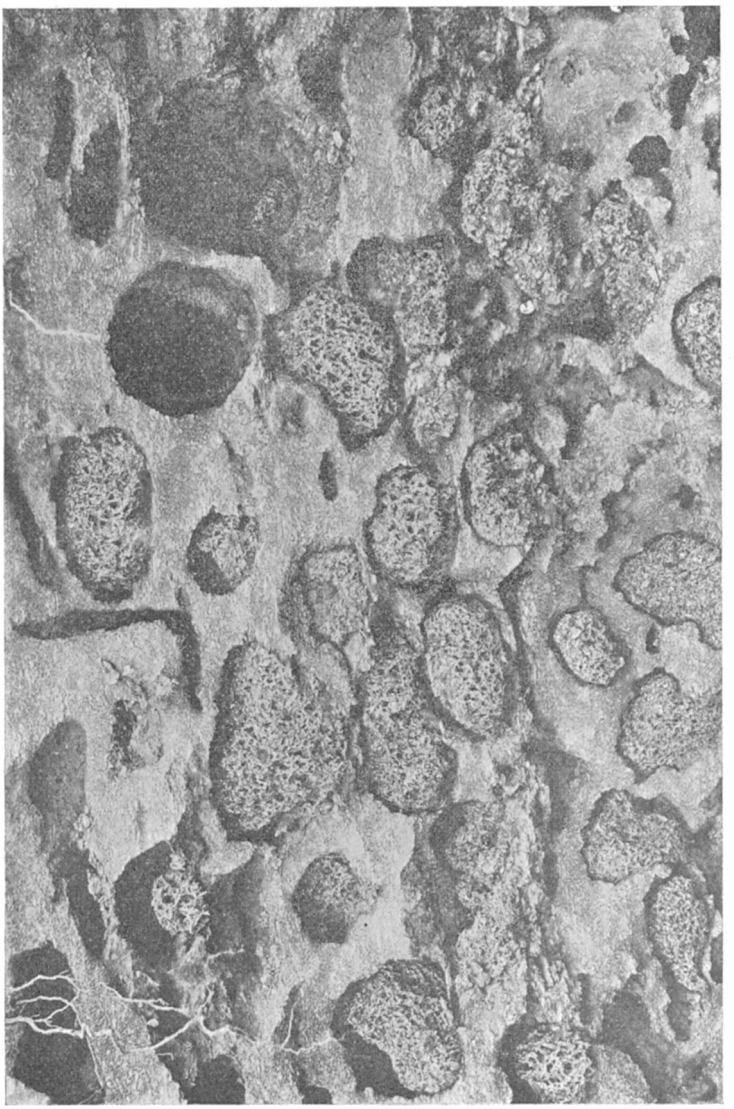

FIG. 69

Portion of nest of *Atta vollenweideri* shown in Fig. 68, more enlarged to show the sponge-like fungus-gardens *in situ* in the chambers. About one eighth natural size . (Photograph by Dr. Carlos Bruch.)

by the ants is indicated by the fact that they do not appear when the fungus is grown in isolation on artificial media. Alfred Moel-

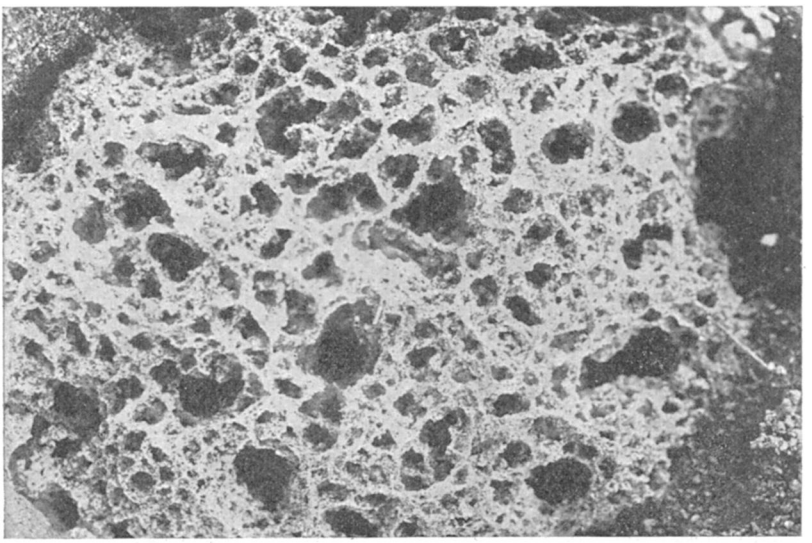

FIG. 70

Portion of fungus garden of the Texan leaf-cutting ant (*Atta texana*). About one half natural size.

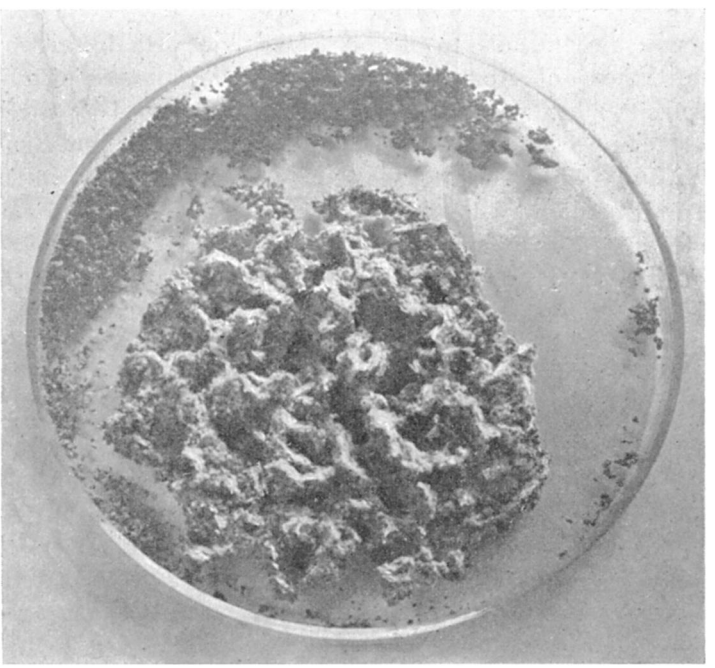

FIG. 71

Fungus garden built in a Petri dish by a colony of Apterostigma in British Guiana. Natural size. (Photograph by Mr. Tee Van.)

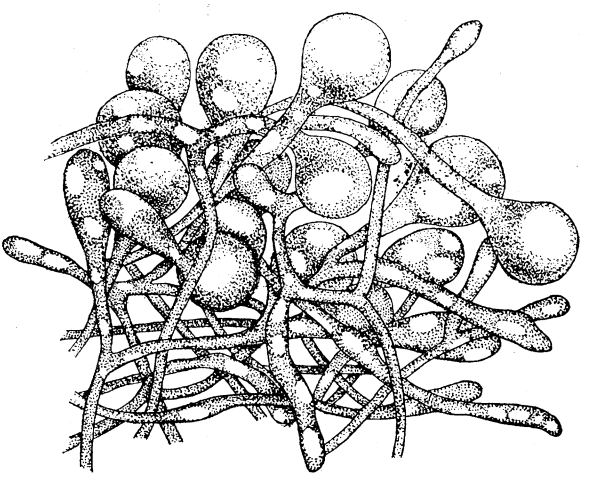

FIG. 72

Modified mycelium (bromatium) of fungus cultivated by the Argentinian *Moellerius heyeri*. The globular swellings of the hyphæ are produced by the ants. (After Carlos Bruch.)

ler, who was the first to cultivate these fungi, regarded them as belonging to the Agarics and named one of them *Rozites gongylophora*. Either the ants prevent the mushrooms from appearing, or, more probably the subterranean conditions under which the mycelium is cultivated are unfavorable to their development. Moeller was also unable to obtain the mushrooms in his cultures, but found those of Rozites growing on the surface of an abandoned Acromyrmex nest. That the fungi cultivated by the various Attiini belong to several different genera is shown by Bruch and Spegazzini who have recently been able to identify the mushrooms of the fungi cultivated by several Argentinian Attiini. *Acromyrmex lundi*, e. g. cultivates *Xylaria micrura* Speg., *Moellerius heyeri*, *Poroniopsis bruchi* Speg. and *Atta vollenweideri*, a gigantic Agaric, *Locellina Mazzuchii* Speg. (Fig. 73).

The lower genera of the Attiini differ in many particulars from such highly specialized forms as Atta and Acromyrmex. Their nests are smaller and there are differences in the gardens and the substratum, or substances on which the fungi are grown. The species of Trachymyrmex suspend the garden from the ceiling of the nest chamber instead of building it on the floor, and in some species of Apterostigma it is enclosed in a spherical envelope of dense mycelium, so that, except for its larger size, it much resembles the silken egg-case of a spider. These ants and others, such as Cyphomyrmex and Myrmicocrypta, use the excrement of other insects, especially of caterpillars, as a substratum for the gardens, and one species, *Cyphomyrmex rimosus*, cultivates a very peculiar fungus (*Tyridiomyces formicarum* Wheeler), which does not grow

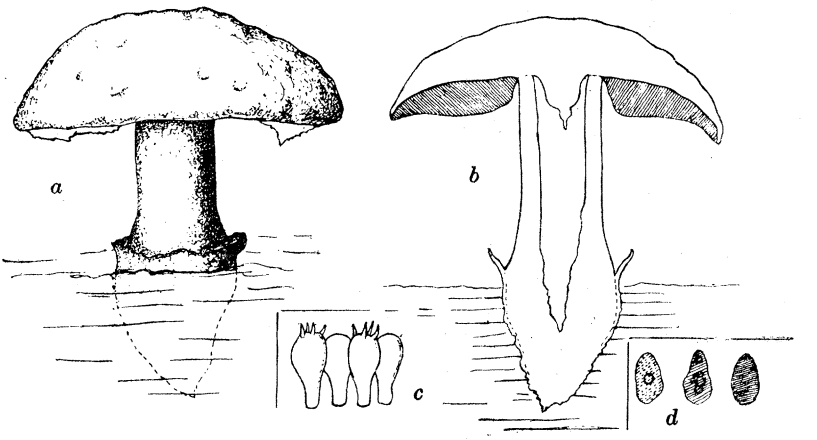

FIG. 73

a, Locellina Mazzuchii the gigantic fruiting phase (pileus 30 to 42 cm. in diameter!) of the fungus cultivated by the Argentinian leaf-cutting ant (*Atta vollenweideri*); *b*, section of same; *c*, basidia; *d*, spores. (After C. Spegazzini.)

in the form of a mycelium but of isolated, compact bodies, resembling little pieces of American cheese, and consisting of yeast-like cells. The same or a very similar fungus is grown by the species of Mycocepurus.

How do all these Attiine ants come into possession of the various fungi which they cultivate with such consummate skill. The question is, of course, twofold, since we should like to know how the individual colony obtains its fungus and how the ancestors of the existing Attiini first acquired the fungus-growing habit. The former question has been answered by the very interesting investigations of Sampaio, H. von Ihering, J. Huber and Goeldi on the Brazilian *Atta sexdens* and of Bruch on the Argentinian *Acromyrmex lundi.* The virgin queen of these species, before leaving the parental nest for her marriage flight, takes a good meal of fungus. The hyphæ, together with the strigil sweepings from her own body and, according to Bruch, also some particles of the substratum, are packed into her infrabuccal pocket, where they form a large pellet, which she retains till she has mated, thrown off her wings and made a small chamber for herself in the soil. She then casts the pellet on the floor of the chamber where its hyphæ begin to proliferate in the moist air and draw their nutriment from the extraneous materials with which they are mingled (Fig. 74*A*). The queen carefully watches the incipient garden and accelerates its growth by manuring it with her feces (*C* and *D*). She begins to lay eggs (Fig. 76 *A*) and even breaks up some of them and adds them to the garden, which soon becomes large enough to form a kind of nest for the intact and developing eggs (Fig. 74 *B* to *F*).

The young larvæ on hatching proceed to eat the mycelium and eventually pupate and emerge as small workers, which break through the soil, bring in pieces of leaves and add them to the garden. The care of the latter then devolves on the workers and the queen henceforth devotes herself to laying eggs. The colony is now established and its further development is merely a matter of enlarging the nest, multiplying the gardens and increasing the population. Thus Atta and Acromyrmex transmit their food-plants from generation to generation in a very simple manner, that is, merely by the queen's retaining, till she has established her nest chamber, the infrabuccal pellet consisting of her last meal in the colony in which she was reared. And there is every reason

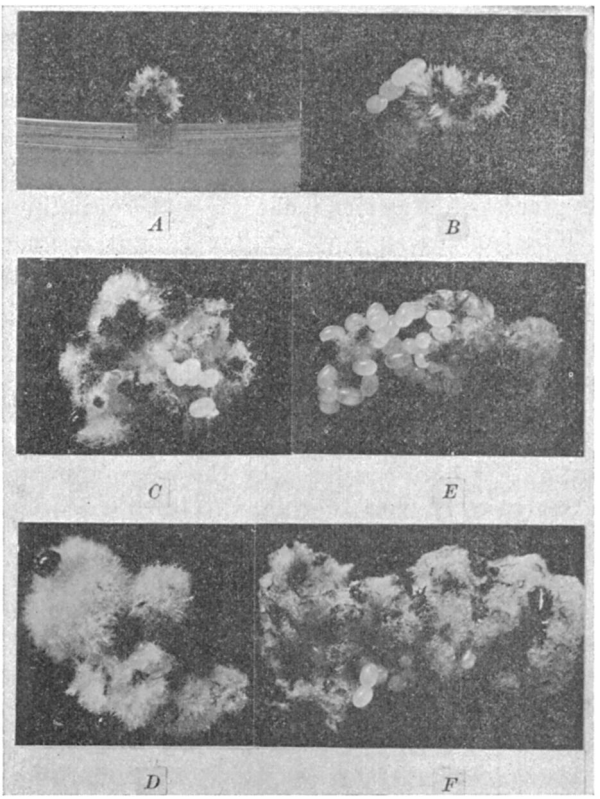

FIG. 74

Stages in the development of the fungus garden by the queen of the Argentinian *Moellerius hyeri*. *A*, pellet of substratum 36 hours after its ejection from the queen's infrabuccal pocket. The hyphæ have begun to grow. *B*, same pellet after 3 days, with 4 eggs; *C*, same pellet after 8 days, showing droplets of feces with which the queen manures the hyphæ. *D*, same pellet after 12 days, also showing droplets of feces; *E*, small fungus garden after 30 days, with 32 eggs; *F*, same after 40 days. The magnification of all the figures is very nearly 10 diameters. (Photographs by Dr. Carlos Bruch.)

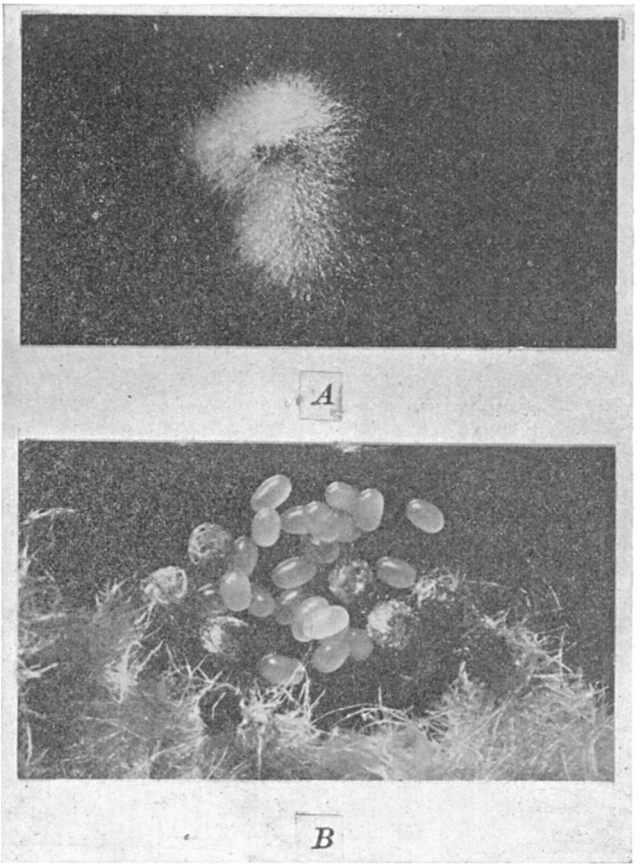

FIG. 75

A, an infrabuccal pellet of the queen *Moellerius heyeri* after cultivation for 36 hours on gelatine. X10. *B*, eggs and pellets made of filter paper by a queen *Moellerius heyeri* that had failed to develop a fungus garden. X10. (Photograph by Dr. Carlos Bruch.)

to suppose that the same method of transmitting the fungus from the maternal to the daughter colonies is practiced by all the other genera of the tribe.

Of course, the answer to the question as to how the ancestors of the Attiini acquired their food-fungi in the first place must be purely conjectural. Yet certain observation by Professor I. W. Bailey and myself seem to indicate from what simple beginnings the elaborate fungus-growing habits may have been evolved. An examination of the infrabuccal pellets of the most diverse ants shows that in nearly every case they contain fungus spores or pieces of mycelium collected from the surfaces of their bodies or from the walls of the nest. Moreover, many ants have a habit of casting their pellets on the refuse heaps, or kitchen-middens of their nests, and Professor Bailey finds that in the case of certain African

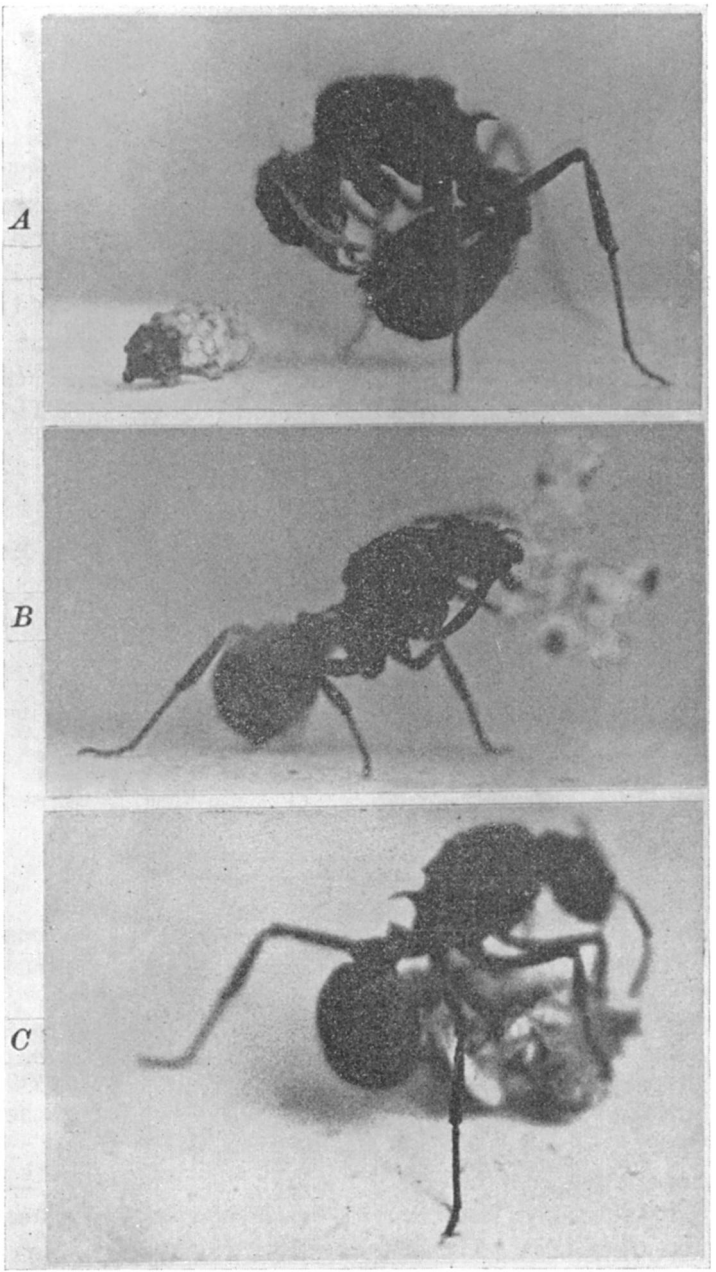

FIG. 76

Behavior of the queen of *Moellerius heyeri*. *A*, photographed in the act of laying an egg. The incipient fungus garden in which the egg will be placed is shown to the left resting on the floor of the nest chamber; *B*, queen placing an egg in the fungus garden which is sticking to the glass wall of the artificial nest. *C*, queen photographed in the act of placing a droplet of feces in the fungus garden. Magnification 5 diameters. (Photographs by Dr. Carlos Bruch.)

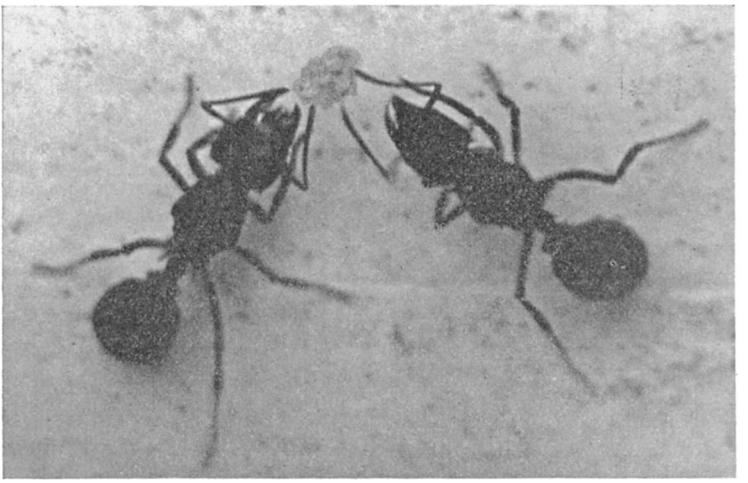

FIG. 77

Two friendly queens of *Moellerius heyeri* caring for a single incipient fungus garden, which is adhering to the glass wall of the artificial nest X5. (Photograph by Dr. Carlos Bruch.)

Crematogasters that live in the moist cavities of plants (Plectronia, Cuviera) the refuse heaps consist very largely of such ejected pellets and produce a luxuriant growth of aërial hyphæ which are cropped by the ants. From such a condition it is, perhaps, only a short step to the establishment of small gardens consisting at first of the pellets and later of these and accumulations of extraneous materials, such as the feces of the ants, those of caterpillars and beetles, vegetable detritus, etc., which might serve to enlarge the substratum and increase the growth of the fungus. The selection of particular species of fungi and their careful culture and transmission are evidently specializations that must have been established before the stages represented by even the most primitive existing Attiini could have been attained.

Whatever may have been the processes whereby the ancestral Attiini developed the fungus-growing habit, it must have originated in the more humid portions of the tropics, since nearly all the more primitive species of the tribe are still confined to the rain-forests. But certain species soon found that by sinking their galleries and chambers to a greater depth in the soil they could easily carry on their fungus farming even in arid regions. Thus some species of Moellerius, Trachymyrmex and Cyphomyrmex have come to live in the dry deserts of Arizona, New Mexico and northern Mexico, and as they can always find in such localities enough vegetable material for the substrata of their gardens, they have attained to a control of their environment and food-supply, which even the human inhabitants of those regions might envy.